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THE PHYSIOLOGY, LIFE CYCLES AND PHYLOGENY OF THE PARASITIC FLATWORMS[1]

BY HORACE W. STUNKARD

The present account is restricted to those classes of the phylum Platyhelminthes whose members are obligate parasites. This arbitrary limitation is made despite the obvious fact that many of the turbellarians are parasitic and that the exclusively parasitic groups have a common ancestry with the Turbellaria. Although the forms are genetically related, the free living and parasitic species are so unlike in life history and metabolic activities that they constitute two distinct groups, so widely separated that the characteristics and methods of study applicable to one are entirely inadequate for the other.

The adoption of the parasitic habit has led to modification of the parasite, particularly the digestive and reproductive systems, with attendant alterations in metabolism and in the course of the life cycle. Ordinarily the worm becomes sexually mature in or on a definite organ and passes the remainder of its life there. For perpetuation of the species, it is essential that dispersal stages of the parasite leave the definitive host and accomplish the infection of new hosts. If two or more host species are required to complete the life cycle, there may be a corresponding number of infective larval stages. In the long period of evolutionary history there have been many changes in the relations between hosts and parasites. While there is much uncertainty concerning the phylogeny of the parasitic flatworms, it is patent that parasitic species have been derived from free living ancestors and that present life cycles are in many cases very different from the original ones. Former hosts have become extinct and certain of their parasites, modified in form and life history, have passed on to other hosts. Moreover, former hosts, serving as food for other animals, have carried their parasites into new host species where they have become established. Such a history has led to alternation of hosts and the interpolation of new hosts, to accessory methods of reproduction, to metamorphosis and peculiar types of metagenesis.

The profound changes which have occurred in the life cycles and

[1]Contribution from the Biological Laboratory, New York University, and the Department of Lower Invertebrates, The American Museum of Natural History.

metabolism of parasitic species have so modified their physiological requirements that they have become incapable of free-living existence and are dependent on their hosts for nourishment. The problem is complicated by the fact that the life cycles of most parasitic flatworms comprise two or more successive generations which may infest different host species and for which the essential conditions and nutritional demands may be very dissimilar. Their physiology has been studied very little and the factors which determine host-parasite specificity are quite unknown. The basis of the relationship is chemical and the adjustment has developed gradually during a long period of association. Certain parasites manifest very rigid host-parasite specificity while others may complete their development in a variety of different hosts.

An excellent review of present knowledge concerning the respiration, metabolism and nutrition of parasitic worms was made by McCoy (1935). The normal habitat of these worms is varied and those which live in the intestine must exist in the virtual absence of oxygen. Biochemical studies on *Fasciola hepatica*, *Moniezia expansa* and *Triaenophorus nodulosus* have shown that they live equally well in the presence or absence of oxygen. Under anaerobic conditions the worms consume glycogen with the production of CO_2 and fatty acids while in aerobic conditions the consumption of oxygen varies directly with the oxygen tension of the medium. The CO_2 production is the same under anaerobic and aerobic conditions and bears no constant relation to the oxygen consumption. The exact rôle of oxygen in metabolism is doubtful and all of the results are subject to the criticism that the experiments were not performed under sterile conditions. It is impossible at present to determine to what extent the results have been influenced by the activities of bacteria. Since cestodes have no alimentary tract, their nutrition must be entirely saprophytic, while the nutritional requirements of trematodes probably vary in different species. Certainly the flukes which infest the lungs, blood vessels, intestine, liver and urinary bladder live in very diverse habitats. To what extent digestion is extracellular or intracellular, and whether the worms utilize only soluble products or whether they feed on cells and tissue exudates, is as yet uncertain.

Since the environmental conditions are so unlike during different periods of the life cycle, the physiological processes of parasitic flatworms must vary to a considerable degree. There is much evidence that the worms are not deleteriously affected by wide variations in environmental conditions, and changes in such factors as pH, CO_2, temperature and constitution of the external milieu may have only slight effects. In

contrast to these observations is the well-known host-parasite specificity which in certain instances almost limits a particular parasite to a single host species.

None of the parasitic flatworms has ever been raised in artificial media and at present the only feasible method of culturing these animals is to maintain them in or on appropriate hosts. Attempts to grow them *in vitro* have resulted in failure, largely because there is no adequate knowledge of their metabolic requirements. Attempts to culture these parasites have been confronted by two horns of a dilemma. The worms cannot be maintained *in vitro* because their physiology is so imperfectly understood, and their physiological processes cannot be subjected to controlled study since the worms cannot be maintained under experimental conditions. The writer (1930, 1932) has reported attempts to culture the trematode *Cryptocotyle lingua* and the cestode *Crepidobothrium lönnbergi* in nutrient media. This trematode was selected because it does not have a rigid host specificity and develops in many animals. Furthermore, it reaches maturity in about six days. Various methods were tried to secure specimens free from bacteria, but none was entirely successful. The worms not only failed to grow, but actually diminished in size during the experiment. *Crepidobothrium lönnbergi* was selected because it is parasitic in a poikilothermous animal and the experiments could be conducted at room temperature. In this species some growth and development was obtained, but the strobilas were abnormal in appearance and the proglottids were sterile. Although these studies attained little in the way of successful results, they indicate that the problem can be solved. The development of techniques by which metazoan endoparasites can be grown in artificial media would be a most important step in the advancement of knowledge of the parasitic flatworms.

The life cycles of most species are complicated and it is only in recent years that substantial progress has been made in the elucidation of the successive developmental stages. Indeed, most of the known life histories have been discovered in the last ten years, and the number of life cycles which have been experimentally demonstrated is exceedingly small when compared with the number as yet unknown. Among the developmental cycles which have been reported, many are incompletely described. Frequently only a portion of the cycle is sketched with suggestions concerning the probable course of development. A further distressing situation results from the fact that it is often extremely difficult to complete known life histories under laboratory conditions.

All members of a natural family follow a similar course of development and it has become clearly evident that types of life cycle are closely correlated with phylogenetic and systematic relations of the worms. The life cycles of animals, and especially parasitic ones, provide the best evidence of their genetic relations and systematic position. Actually, in species which have undergone excessive adaptation, the developmental stages afford the only adequate and satisfactory data on which to base a determination. The pronounced degeneration of many parasitic flatworms, involving the more or less complete loss of the digestive tract and the interpolation of accessory methods of reproduction, indicate a very long period of parasitic existence. Evidence of the remote origin of the digenetic trematodes was noted by Stunkard and Shaw (1931) from the observation that closely related species infest marine and fresh-water hosts that have been distinct since the Mesozoic era.

If habitat, degree of degenerative change and extent of adaptation are taken as criteria, the parasitic flatworms may be arranged in the following sequence: Mesozoa, Cestoidea and Trematoda. Each of the classes is composed of two more or less distinct groups. The Mesozoa contain the orders Rhombozoa and Orthonectida; the Cestoidea comprise the subclasses Cestodaria and Cestoda; while the Trematoda contain the subclasses Digenea and Monogenea. The Mesozoa are simple degenerate organisms, which infest marine invertebrates, and which have probably been parasitic since early geologic periods. The Cestoidea, perhaps less ancient, were originally parasites of invertebrates and most of them still pass their early developmental stages in arthropods or annelids. The subclasses of the Trematoda are not closely related, since the Digenea were probably parasites of molluscs before the advent of higher vertebrates, while the Monogenea have adopted the parasitic habit at a more recent period and infest only vertebrate hosts.

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MESOZOA

The name Mesozoa was proposed by Éd. van Beneden (1876) to denote a group of organisms which he regarded as intermediate between Protozoa and Metazoa. These animals were discovered in the renal sacs of cephalopod molluscs by Krohn (1839) and had been studied by Kölliker (1849), Wagener (1857), Claparède and Lachmann (1861), Lankester (1873) and P. J. van Beneden (1875). É. van Beneden characterized the Mesozoa as animals without germ layers or gastrula formation, and originally the group contained only the dicyemids. The orthonectids were discovered by Keferstein (1868) and the study of these animals by McIntosh (1874), Giard (1877, 1879) and Metschnikoff (1881) led to their inclusion in the Mesozoa. Other inadequately described species have been appended tentatively to the group.

The zoölogical position of the Mesozoa is yet uncertain and students of these parasites have held very different opinions concerning their true status. Claparède and Lachmann related them to the Infusoria and particularly to the Opalinidae. P. J. van Beneden placed them with the gregarines and Foettinger (1881) listed them as parasitic Infusoria. Hatschek (1888) noted the similarity between these organisms and the planula stage of certain Cnidaria and proposed for them the name Planuloidea, as an appendix to the Coelenterata. Lameere (1918, 1922) advanced an ingenious and plausible thesis relating the Mesozoa to the echiurids. He stated (1922, p. 784), "Les prétendu Mésozoaires sont par conséquent des Vers du groupe des Échiuriens dérivés du genre *Bonellia*, chez lesquels le nanisme et la dégénérescence accompagnant la vie parasitaire ont affecté la femelle aussi bien que le mâle." Metschnikoff (1879), Giard (1879), Leuckart (1882), Braun (1893) and other parasitologists have considered the Mesozoa as degenerate flatworms.

Two excellent studies on the dicyemids of the Mediterranean and of the Pacific coast of North America, respectively, were done by the eminent American zoölogists, Whitman (1882) and Wheeler (1899). Both opposed the idea of van Beneden to establish a separate subkingdom for the Mesozoa and Whitman, after a careful embryological study, concluded: "I see no good reason for doubting the general opinion that they are Plathelminths degraded by parasitism."

In a recent monograph Hartmann (1925) contended that the Mesozoa cannot be compared either with a planula or with an epibolic gastrula, nor with any developmental stage higher than a morula. He maintained that their organization is definitely more simple than that of true

Metazoa in which a gastrula appears in development. Furthermore he stated that they manifest a "primary" alternation of generations and a primitive agametic type of reproduction which occurs among the Protozoa but not among the Metazoa. The concept of Hartmann is very similar to the original one of van Beneden. Hartmann defined the Mesozoa as multicellular animals of morula-like form, which consist of a somatoderm and a reproductive organ, and which have a "primary" alternation of generations. According to him the Phylum Mesozoa contains a single class, the Moruloidea, with two orders, Rhombozoa and Orthonectida. In the Rhombozoa he listed two families, Dicyemidae and Heterocyemidae. It should be noted, however, that the family Heterocyemidae contains only the two genera *Conocyema* and *Microcyema.* Since the name of the family must be formed from the stem of the name of the type genus plus the ending IDAE, it is apparent that the name Heterocyemidae is not valid. For the family Heterocyemidae of Hartmann, I propose the name Conocyemidae with *Conocyema* as the nomenclatorial type. Similarly, in the Orthonectida, Hartmann recognized the family Orthonectidae in which he included the two genera *Rhopalura* Giard and *Stoecharthrum* Caullery and Mesnil. For this family I propose the name Rhopaluridae. Furthermore, Hartmann listed the family Heteronectidae, with a single genus *Pelmatosphaera.* Since this family contains a single genus, the name of the family must become Pelmatosphaeridae. Hartmann described the reproductive stages of the Dicyemidae which occur in the mollusc but admitted uncertainty concerning the method by which new infections are established. He declared that it is impossible, because of their parasitic mode of life, to determine whether the organization of the Dicyemidae and Orthonectidae is progressive or retrogressive, but that in a taxonomic treatment of the Mesozoa it is not essential to determine whether their simplicity is primitive or secondary.

On the last two points the opinion of Hartmann appears to be at variance with established biological principles. The ideas advanced by Hartmann were presaged and proscribed by the statement of Whitman (1882), "Thus far no objection has been raised to the creation of a middle division of the animal kingdom on the ground that all the assumed representatives of this division are parasites. But I think this must be admitted to be one of the unfortunate aspects of the case, although we may not be able to point to undeniable evidence of degeneration. But who will venture to assert, before applying the hypothesis of 'degenerative evolution,' it is indispensable to find unmistakable marks

of degeneration, such as are seen, for example, in the development of *Sacculina*, *Lernaeocera*, *Barnacles*, etc.? That this hypothesis admits of a very wide application to the simpler forms of life has been made sufficiently clear by Dohrn (27) and Lankester (40). When we find an animal in the form of a simple sack, filled with reproductive elements, secured by position against enemies, supplied with food in abundance, and combining parasitism with immobility, we have strong reasons for believing that the simplicity of its structure is more or less the result of the luxurious conditions of life which it enjoys, even if its development furnishes no positive evidence of degeneration." In addition to the strong presumptive evidence cited by Whitman, there are certain features which may be regarded as positive evidence of parasitic degeneration, but a final decision can be reached only when the development of the Dicyemidae is completely known. If parasitism has led to progressive evolution in the Mesozoa, as suggested by Hartmann, it is a most unusual and remarkable occurrence, and one that could be accepted only when supported by incontestable proof. All available evidence appears to indicate that the simplicity of the Mesozoa is secondary and the result of parasitic adaptation. If it should be established that the simplicity is not primitive, the basis of Hartmann's classification would disappear, together with his assertion that the nature of the simplicity (whether primitive or secondary) may be disregarded in systematic considerations.

For the present at least, I am disposed to regard the Mesozoa as degenerate or highly specialized flatworms, derived not from any existing group of the Turbellaria but from a very remote ancestor of all existing flatworms. They probably branched off a primitive stem before the origin of the digenetic trematodes or cestodes. The free swimming larvae are modified planulae and bear many resemblances to the larvae of the trematodes.

RHOMBOZOA

These organisms occur on the venous appendages of the excretory organs of cephalopod molluscs. Their life cycle is very imperfectly known. The development of the successive stages in the mollusc has been described by several authors, but there is much difference of opinion concerning the infusorigen and infusiform stages. Earlier authors described the infusorigen individuals as females and the infusiform embryos as males, but Lameere (1918, 1922) contended that the infusorigens are hermaphroditic, that there are no males, and that the infusiform is

an infective stage which leaves the cephalopod and transmits the infection to a new host. He advanced the hypothesis that the infusiform may enter some host other than a cephalopod and that there may be another generation or series of generations in an as yet unknown host. The observations of Lameere concerning the sequence of stages in the mollusc confirmed those of Wheeler (1899). The recent studies by Nouvel (1929, 1932, 1933) support the opinion of Lameere concerning the life cycle.

ORTHONECTIDA

The Orthonectida are parasites of planarians, nemertines, annelids, echinoderms and molluscs. There is an alternation of generations; the sexual phases are free living in the sea and the asexual stages occur in plasmodia in the tissues of various animals. In dioecious species the males and females are distinguished by differences in size and form. Certain species are hermaphroditic and it is believed that the monoecious condition is secondary, although the development of the sexual conditions is not well known. In a recent paper Atkins (1933) described the successive stages and swimming behavior of *Rhopalura granosa*, a species which infests the lamellibranch mollusc, *Heteranomia squamula*.

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CESTOIDEA

This class of the Platyhelminthes is extensively adapted to the parasitic habit. Except for the occasional appearance of ephemeral larval stages these worms are endoparasites, and all traces of a digestive system have disappeared. With rare exceptions, the adult stages live in the intestine of vertebrates. The mature worms lack sense organs and the body is covered with cuticula. Typically the body consists of scolex, neck and

strobila, although any one of these parts may be absent. Except for species of the genus *Dioecocestus*, all members are hermaphroditic. In monozoic species there is a single set of male and female reproductive organs, while in merozoic ones the gonads are serially repeated in more or less completely distinct proglottids. Occasionally the male and female organs may be duplicated in each proglottid. The Cestoidea may be arranged in two subclasses, Cestodaria and Cestoda.

CESTODARIA

The Cestodaria are a small group of monozoic forms in which the larva (Lycophora) contains ten hooks. There are two orders, Amphilinidea and Gyrocotylidea, each composed of a single family. The Amphilinidae are parasitic in the body cavity of ganoid fishes, the Gyrocotylidae in the intestine of selachians. Members of the Amphilinidae occur infrequently in the body cavities of teleost fishes and according to Woodland (1923) the worms, when sexually mature may bore through the body wall. In ganoid fishes, eggs of the parasite pass out through the abdominal pores. The life cycle of *Amphilina foliacea* was discovered by von Janicki (1928). Eggs of the parasite are eaten by species of *Gammarus* and related crustaceans; the embryos develop in the body cavity to the plerocercoid stage. Since the final hosts feed on these crustaceans it is probable that no other host is required. The early stages in the life history of *Gyrocotyle* were described by Ruszkowski (1931).

The older authors and more recently Woodland (1926) regarded all monozoic species as members of the Cestodaria. Lühe (1910), Nybelin (1922), Hunter (1930) and Fuhrmann (1931), however, considered the Caryophyllaeidae as secondarily monozoic and members of the Pseudophyllidea.

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CESTODA

The subclass Cestoda contains a large assemblage of species, all of which, with the exception of those in the family Caryophyllaeidae, are merozoic and form a more or less distinct strobila. The larva (Onchosphaera) contains six hooks and lacks the clear structural differentiation of the Lycophora. There are five orders and the life histories in each will be discussed separately.

The metabolism of cestodes is obscure and there is no satisfactory explanation why the living worms are not digested in the intestine of their host. Since cestodes have no digestive tract, their nutrition must be entirely saprophytic. Their nutritional requirements cannot be very rigid, however, since the content of the alimentary tract is inconstant in amount and character and the worms are normally subjected to greatly varying conditions. Numerous attempts have been made to maintain these worms *in vitro* but the results, from those of Lönnberg (1892) to those of Wardle (1934), have been disappointing. The latter paper contains a good bibliography.

TETRAPHYLLIDEA

Members of the order Tetraphyllidea occur in the intestine of fishes, amphibians and reptiles. The Phyllobothriidae, Onchobothriidae, Lecanicephalidae, Cephalobothriidae and Discocephalidae infest selachian fishes, while the Monticellidae parasitize siluroid fishes. Members of the family Proteocephalidae (Ichthyotaeniidae) occur in fresh-water fishes, amphibians and reptiles. Larvae of the marine species have been found in copepods and later stages in teleosts, molluscs and larger crustaceans. No life cycle has been completely traced but there is evidence of asexual multiplication of the larvae and it is probable that two intermediate hosts are involved.

In the family Proteocephalidae, the life history of several species has

been discovered. An account of the early work is contained in the paper by Essex (1928*a*). The complete life cycle of *Proteocephalus filicollis* was traced by Meggitt (1914). Sexually mature stages occur in the stickleback and *Cyclops varius* was found to be the first and only intermediate host. A similar life cycle was described by Wagner (1917) for *Proteocephalus torulosus.* Adult worms infest *Cyprinus orfus* while *Cyclops strenuus* and *Diaptomus castor* serve as first intermediate hosts. Kuczkowski (1925) found that the larvae of *P. percae* and *P. longicollis* develop in species of *Cyclops.* Essex (1928*a*) described the life history of two species of *Corallobothrium* which occur in catfishes. Infection was produced in species of *Cyclops* by feeding eggs of the cestodes. The infected cyclops were fed to minnows, *Notropis blennius,* and the larvae were recovered from the body cavity. Catfishes became infected by eating either the infected cyclops or infected minnows. Essex showed that ordinarily two intermediate hosts are involved in the life cycle although the second intermediate or transfer host is not absolutely essential. Apparently the larvae develop only in particular species of crustaceans and if these crustaceans are eaten by an animal other than the normal host the larvae bore from the intestine to the body cavity. In the normal host they remain in the lumen of the intestine and attain sexual maturity. Other recent American contributions include the studies of Hunter (1928, 1929), Magath (1929) and Thomas (1931).

DIPHYLLIDEA

The order Diphyllidea contains a single genus *Echinobothrium.* Sexually mature stages live in the intestine of selachian fishes and larvae of these cestodes have been reported from marine crustaceans and molluscs. Ruszkowski (1927) described the life cycle of *E. benedeni,* in which the larvae were found in the decapod crustacean *Hippolyte varians.* He gave a complete historical review of the group and concluded that there is a single intermediate host.

TETRARHYNCHIDEA

The tetrarhynchid cestodes are principally parasites of selachian fishes although species have been reported from *Silurus glanis* and *Lota lota* in Swiss lakes and *Haplobothrium globuliforme* occurs in the intestine of *Amia calva.* The eggs contain a ciliated larva, coracidium, and larval stages have been reported in the coelom and other organs of holothurians, molluscs, crustaceans and fishes. Although the complete

life history is not known for any of the marine species, Dollfus (1929, 1930) divided the order into two groups; Acystidea, in which the larva is a plerocercoid; and Cystidea, in which the larva is a tailed or tailless cysticercoid (plerocerous). More recently (1935) in a preliminary note he has announced the inaccuracy of this arrangement. The life cycle of *H. globuliforme* is known through the studies of Essex (1929) and Thomas (1929). The coracidium is eaten by species of *Cyclops* and the second larval stage occurs in the liver of *Ameiurus nebulosis* and the sunfish. Part of the life cycle of *Grillotia erinaceus* was described by Ruszkowski (1932). The present fragmentary knowledge concerning the development of the tetrarhynchid cestodes indicates that members of this group typically have a three-host life cycle.

PSEUDOPHYLLIDEA

Members of this order infest all classes of vertebrates and one genus, *Archigetes*, contains species, possibly neotenic, which become mature in the coelom of oligochaete annelids. The first life cycle in this order to be experimentally demonstrated was that of *Diphyllobothrium latum*, the human fish tapeworm, by Janicki and Rosen (1917). A more detailed study of the development of this species was done by Vogel (1929, 1930). *D. latum* is now endemic in the United States and a series of studies in this country has confirmed the earlier accounts. Ciliated embryos (coracidia) emerge from the eggs and are eaten by copepods. The larvae bore into the body cavity of the crustacean where they develop into procercoids. The infected copepods are eaten by small fish and the larvae pass into the muscles where they become plerocercoids. If these small fish are eaten by other larger fishes the larvae migrate again to the muscles. When fish containing mature plerocercoids are eaten by the final host the larvae remain in the intestine and develop to sexual maturity. Rosen (1918) described similar life cycles for *Triaenophorus nodulosus* and *Abothrium infundibuliforme* although Fuhrmann (1931) reproduced Rosen's figures of *A. infundibuliforme* and assigned them to the species *Eubothrium crassum* (Bloch). Similar life cycles were described for *Ligula simplicissima* by Rosen (1919); for *Diphyllobothrium mansoni* by Joyeux and Houdemer (1928); for *Diphyllobothrium decipiens* and *D. erinacei* by Li (1929); for *Bothriocephalus cuspidatus* by Essex (1928*b*); for *Schistocephalus solidus* by Callot and Desportes (1934).

While most of the pseudophyllideans have a three-host life cycle, there are some exceptions. The larvae of *Cyathocephalus* occur in

Gammarus and a two-host cycle is indicated. In the aberrant family Caryophyllaeidae the life cycle is reduced. The larvae of *Caryophyllaeus* have well formed gonads while still in the coelom of oligochaete annelids and it is most unlikely that a third host is required. The researches of Wisniewski (1930) have shown that in the genus *Archigetes*, the life cycle is completed in a single host species.

CYCLOPHYLLIDEA

Among cyclophyllidean or taenoid cestodes ordinarily only one intermediate host is necessary. These worms have three stages in the life cycle. The eggs develop within the uterus of the worm until they contain infective larvae. Such embryonated eggs, either separately or contained within a segment of the worm, pass from the intestine of the primary host and, with rare exceptions, develop further only when ingested by a suitable intermediate host.

In the intestine of the intermediate host the onchospheres emerge, and by use of their hooks, penetrate the intestinal wall. If the intermediate host is an invertebrate, the onchospheres invade the body cavity and complete the second stage of their life cycle, developing into cysticercoid larvae. Typically, these larvae have more or less solid bodies and caudal appendages or cercomeres in which the six hooks of the first larval stage may be cast off. The body develops the scolex of the future cestode with its adhesive organs, ready for attachment when introduced into the intestine of the primary host. Cysticercoid larvae occur chiefly in invertebrate hosts, and they have been found in crustaceans, insects, myriapods, oligochaetes, leeches and molluscs.

In case the intermediate host is a vertebrate, the onchospheres on piercing the intestinal wall reach the lymph spaces or veins and pass by way of the portal system to the liver. They may continue their development to the next infective stage in the liver or they may pass to other organs. These larvae develop fluid filled vesicles and are known as cysticerci or bladder worms. In any event, the second stage in the life cycle is completed when the larva, either cysticercus or cysticercoid, has developed sufficiently to be infective for the primary host.

The third stage of development occurs in the intestine of the primary host. When the cysticercoid or cysticercus is ingested, larval coverings if present are digested; the larva attaches itself to the intestinal wall and develops into the sexually mature cestode.

From known life histories a few generalizations may be made. The onchosphere is exceedingly delicate, quite incapable of independent

existence. It is always passively introduced within its coverings into the the intestine of the next host. Ordinarily it does not spontaneously emerge except in the intestine of an appropriate intermediate host. The onchosphere will not remain in the intestine, but always penetrates the wall to reach the body cavity or other organs where development proceeds. With rare exceptions, multiplication does not occur in the larval stage. In almost all known life histories, the larva after developing to an infective stage in a suitable intermediate host, is accidentally ingested by the final host with food, and sexually mature cestodes are usually found in carnivorous vertebrates.

In a few instances, viz., species of *Hymenolepis* and *Cylindrotaenia*, direct development may occur without the intervention of an intermediate host. When eggs are ingested by the primary host, the onchospheres emerge, bore into the wall of the intestine, and continue their development there. On reaching the infective stage they return to the intestine where they become sexually mature. In these cases development is completed in a single host species, the larval stage in the intestinal wall and the adult stage in the lumen. Presumably these abbreviated life cycles have arisen by the dropping out of a former intermediate host and it is possible that certain of the species in question may develop with an intermediate host as well as directly (Bacigalupo, 1931).

The life cycles which have been demonstrated are too numerous to list separately and the study dates back to the classical investigations of Leuckart, Moniez, Grassi and others. The early literature is reviewed in the monographs of Braun (1894–1900) and Joyeux (1920). More recent life cycles are described in the monograph by Fuhrmann (1931).

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TREMATODA

The trematodes were classified according to adhesive organs until van Beneden (1858) divided them into two groups on the basis of life history. One group, the Monogenea, consists of species which have a direct development and infest a single vertebrate host; whereas the other, the Digenea, contains species which have an indirect, a metagenetic, or more properly an alloiogenetic development, and in which the successive stages of the life cycle are harbored by two or more host species. In the Digenea sexually mature adults infest the intestine or body cavities of vertebrates, while asexual multiplication occurs in the gonads and digestive glands of various species of molluscs. Other differences were noted, viz.: the monogenetic forms are ectoparasitic and possess multiple adhesive organs, whereas the digenetic trematodes are endoparasitic and the adhesive structures consist typically of an oral sucker and an acetabulum. Thus the Monogenea comprise the polystomes and the Digenea comprise the distomes and monostomes of other authors. Nevertheless, van Beneden regarded the differences in type of development and life history as of paramount importance and subsequent investigations have abundantly confirmed his conclusion. Two seeming exceptions are undoubtedly secondary and more apparent than real; among the Digenea, members of the family Aspidogastridae are monogenetic, and among the Monogenea, the polystomes of amphibians are digenetic. It appears certain, however, that the two great groups of trematodes are only very distantly related, if indeed they have not descended from unlike turbellarian ancestors, and it is probable that the digenetic forms were parasitic in molluscs before the advent of higher vertebrates.

DIGENEA

Thousands of digenetic trematodes are known by their sexually mature stages and in recent years the asexual stages have received increased attention. The first complete life history to be experimentally demonstrated was that of *Fasciola hepatica*, the liver fluke, done independently by Leuckart (1882) in Germany and by Thomas (1883) in England, which still remains the usual text book example of digenetic trematode development. It has been demonstrated repeatedly that the members of the Digenea in their development conform to a common method; migrations by primary larval forms (miracidia) transferring the parasites from vertebrate to molluscan hosts, where a series of asexual generations produce other and different larval forms (cercariae), which either directly or indirectly return again to their vertebrate hosts. For many years the identification of particular larval stages with their adult forms was difficult and slow but the last ten years especially have witnessed an outburst of successful life history studies and the addition of a wealth of new information.

Mathias (1925) described the successive stages in the life cycle of three species and listed twenty-five additional ones for which the life history had been more or less completely described. An extensive list of the literature on the Digenea is given in the excellent monograph of Fuhrmann (1928). The life cycles that had been solved in the United States previous to 1929 were listed by Stunkard (1930). In that paper he described the life cycle of *Cryptocotyle lingua*. Other life history studies done at about this time were those of Woodhead (1929) on *Bucephalus papillosus*, of Palombi (1929) on *Helicometra fasciata* Rud., of Beaver (1929) on *Allassostoma parvum* Stunkard, of Azim (1930) on *Echinostomum recurvatum*, of Palombi (1930) on *Diphtherostomum brusinae* Stossich, of Brumpt (1930) on *Schistosoma bovis*, of Van Haitsma (1930) on *Cotylurus michiganensis*, of Krull (1930) on *Pneumonoeces medioplexus* and *P. parviplexus*, of McCoy (1930) on two species of *Hamacreadium*, of Mathias (1930) on *Notocotylus attenuatus*, of Sinitsin (1930) on *Fascioloides magna*, and of Woodhead (1930) on other species of *Bucephalus*. In addition there were preliminary notices, reported in more detail later, and some partial life cycles were described.

Subsequent contributions include the life cycles of *Schistosomatium douthitti* by Price (1931), of *Cotylurus flabelliformis* and *Diplostomum flexicaudum* by Van Haitsma (1931*a*, 1931*b*), of *Bilharziella polonica* and *Apatemon gracilis* by Szidat (1931*a*, 1931*b*), of *Lepocreadium album* by Palombi (1931), of two species of *Azygia* by Szidat (1932*a*), of

Tracheophilus sisowi by Szidat (1932*b*), of *Parorchis avitus* by Stunkard and Cable (1932), of *Euparyphium murinum* by Tubangui (1932), of *Diplodiscus temperatus* by Krull and Price (1932), of *Pneumobites longiplexus* by Krull (1932), of *Brachylaemus nicolli* by Joyeux, Baer and Timon-David (1932), of *Ostiolum oxyorchis* and *Zeugorchis syntomentera* by Ingles (1933*a*, 1933*b*), of *Haematoloechus complexus*, *Halipegus occidualis* and *Gorgodera* sp. by Krull (1933*a*, 1933*b*, 1933*c*), of *Proterometra macrostoma* by Horsfall (1933), of *Plagitura parva* and *Cercariaeum lintoni* by Stunkard (1933*a*, 1933*b*), of three species in the subfamily Reniferinae by Talbot (1933), of *Crassiphiala ambloplitis* by Hunter (1933), of North American liver flukes by Sinitsin (1933), of *Macroderoides typicus* by McMullen (1933), of *Prohemistomum vivax* by Azim (1933), of *Euparyphium malayanum* by Rao (1933), of *Euparphium recurvatum* by Răsín (1933), of *Euparyphium ilocanum* by Tubangui and Pasco (1933), of *Lecithodendrium chilostomum* by Brown (1933), and of *Heterophyes heterophyes* by Khalil (1933).

More recent life history studies comprise those of *Clinostomum marginatum* by Krull (1934*a*) and Hunter and Hunter (1934), of *Opisthorchis felineus* by Vogel (1934), of *Nephrostomum ramosum* by Azim (1934), of *Cotylophoron cotylophorum*, *Eustomos chelydrae* and *Gorgodera amplicava* by Krull (1934*b*, 1934*c*, 1934*d*), of *Typhlocoelum cymbium* and *Himasthla quissetensis* by Stunkard (1934*a*, 1934*b*), of *Proterometra macrostoma* by Dickerman (1934) and Horsfall (1934), of *Alaria mustelae* by Bosma (1934), of *Crepidostomum cooperi* and *Megalonia ictaluri* by Hopkins (1934), of the American species of *Paragonimus* by Ameel (1934), of *Cercorchis medius* by McMullen (1934), of *Halipegus occidualis* by Thomas and Johnson (1934), of *Brachylaemus fuscatus* by Joyeux, Baer and Timon-David (1934), of *Bacciger bacciger* by Palombi (1934), of *Panopistus pricei*, *Brachylaemus virginiana* and *Telorchis robustus* by Krull (1935*a*, 1935*b*, 1935*c*), of *Eustomos chelydrae* by McMullen (1935*a*), of *Macroderoides typicus* and *Alloglossidium corti* by McMullen (1935*b*), of *Sellacotyle mustelae* by Wallace (1935), of *Apharyngostrigea ibis* and *Lepoderma ramlianum* by Azim (1935*a*, 1935*b*), of *Notocotylus urbanensis* by Luttermoser (1935), and of *Renifer aniarum* and *Dasymetra villicaeca* by Byrd (1935).

Several of the references listed are abstracts of research, and others are complete papers which supplement earlier preliminary reports. The longer papers contain bibliographies in which additional citations may be found.

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MONOGENEA

The monogenetic trematodes occur frequently on the gills and skin of both marine and fresh-water fishes, and occasionally cause fatal epidemics among young fishes. Species have been found also in the oronasal cavities and urinary bladder of turtles, in the urinary bladder and on the skin of amphibians, and on marine crustaceans and cephalopods.

Studies on the life history of the monogenetic trematodes date from the papers of Zeller (1872*a*, 1872*b*, 1876) but few developmental cycles have been completely traced. The work of Gallien (1935) has confirmed the earlier account of Zeller on *P. integerrimum* and showed an alternation of generations in this species. Other life cycles traced experimentally are those of *Gyrodactylus elegans* by Kathariner (1904), of two species of *Dactylogyrus* by Kulwieć (1927), of *Ancyrocephalus vistulensis* by Siwak (1932), of *Epibdella melleni* by Jahn and Kuhn (1932), and that of *Sphyranura oligorchis* by Alvey (1933).

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SUMMARY AND CONCLUSIONS

The conventional method of dealing with the phylum Platyhelminthes, as employed in text books and treatises on zoölogy, is to discuss the Turbellaria, the Trematoda and the Cestoda in that order, with little or no consideration of the Mesozoa as related organisms. Such a method begins with a discussion of typical free living worms and proceeds through a series of forms showing increasingly adaptive modifications, but it gives little idea of the true relationships, of the time factor concerned, or of the effects of parasitism upon these animals.

From a consideration of the bionomics, life cycles and development of the flatworms, it seems possible to formulate a more adequate and comprehensive concept of the group. The general effects of parasitism must be recognized in a consideration of those groups in which it has become established. There is common agreement that it results in adaptive morphological changes and that eventually it may lead to the acquisition of new and accessory types of reproduction. With these guiding principles in mind, a study of the cleavage, development and morphology of the several groups of flatworms may lead to certain definite conclusions. In those forms in which free living larval stages have been retained it is possible to make direct comparisons of early development, while in many of the cestodes the modifications have in large measure eliminated this method of approach. Other evidence, however, may be utilized in an analysis of the problem and homologous structures give unmistakable clues. In the Handbuch der Zoologie, vol. I, p. 48, Bresslau and Reisinger have presented a clear and convincing argument for the descent of the Platyhelminthes from planula-like ancestors. Their conclusions concerning the relationships between the ctenophores, nemertines and euplatyhelminths are logical and present a natural arrangement of the groups. They state further, p. 50.

"Innerhalb der *Euplathelminthen-Reihe* spricht alles für die Ursprüng-

lichkeit der *Acoela*. Ihnen schliessen sich unmittelbar *die Microstomidae unter den hysterophoren Rhabdocoelen* und die *Allocoele Hofstenia* an. Wie sich die *übrigen Turbellarien* daran anreihen, wird bei der Besprechung der Klasse selbst näher ausgeführt werden. Hier sei nur bemerkt, dass über die *Alloeocoelen* eine schöne Stufenfolge zu den *Tricladen* führt. Die *Polycladen* zeigen in ihrem Gonadenbau noch so ursprüngliche Verhältnisse (Ovarien.), dass wohl nur ein Anschluss an sehr primitive Formen in Betracht kommt. Unter den *Rhabdocoelen* verdienen die Familien der *Graffilliden* und *Anoplodiiden* besonderes Interesse, insofern als von ihnen aus vermutlich die Entwickelung der *Trematoden* ihren Ausgang genommen hat. Nach ihrer ganzen Organisation sind die *Monogenea* wahrscheinlich von *Graffilliden*, die *Digenea von Anoplodiiden* oder *anoplodiiden-ähnlichen Kalyptorhynchiern* (*Rhabdocoela*) herzuleiten. Gut stimmt damit überein, dass gerade *diese Familien das Hauptkontingent an Parasiten unter den Strudelwürmern* stellen. Auch die *Temnocephalen* schliessen sich nahe an diese zu parasitischem Leben neigenden *Rhabdocoelen-Familien* an. Die *Cestodarier* und *Cestoden* stammen ihrerseits vielleicht von *Trematoden* ab; da aber das Rostellum der *Bandwürmer* wahrscheinlich dem Rüssel der *Rhabdocoela Kalyptorhynchia* homolog ist, kann auch daran gedacht werden, die *Cestoden* unmittelbar von *turbellarienartigen* Vorfahren herzuleiten."

The selection and treatment of data by Bresslau and Reisinger are highly commendable and their conclusions are very interesting. Many of them will doubtless be accepted as correct, but the origin of the Digenea from the Anoplodiidae appears to disregard the extent of modification among the digenetic trematodes. The suggestion that the Cestoidea may have originated from the trematodes is subject to the same objection. Furthermore, the derivation of a great group like the cestodes from another already highly specialized parasitic one does not commend itself as probable. The Digenea and Cestoda comprise groups too large, too diverse, and too complex to be satisfactorily derived from a single, existing, turbellarian family.

The Turbellaria have in the main remained free living and consequently they may be expected to resemble the primitive ancestral form of the Platyhelminthes. They are chiefly carnivorous in habit, but as a result of their small size, defenseless condition and negative heliotropism, they secrete themselves in small recesses and often in or on the bodies of larger organisms. From these retreats they make predacious excursions or they may derive food from the secretions of their temporary hosts.

Such a mode of life encourages and facilitates the development of the parasitic habit and in fact the majority of the flatworms have adopted it. These worms demonstrate the course and successive stages of parasitic adaptation and no other phylum presents such a continuous and complete transition from free living existence to parasitism. Throughout their entire history these animals have been forced to conceal themselves and the same influences have been operative more or less continuously. The extensive and pronounced degeneration of some of them indicates the long period in which they have been parasitic. From the evidence at hand it is almost certain that members of the phylum became parasites of invertebrates in early geologic time and it is probable that the Mesozoa are surviving representatives of that early association. It is also probable that the cestodes and digenetic trematodes are survivors from that period, which have later added vertebrate hosts in their life cycles and have become biologically more successful. In later periods other commensal and parasitic groups have arisen, e.g., the Temnocephala which occur chiefly on fresh-water invertebrates and the Monogenea which occur chiefly on marine vertebrates. Accordingly it appears that the Turbellaria, Mesozoa, Cestoda and Digenea have descended concomitantly from a common ancestral group of planula-like ancestors.

A phylogenetic determination must take cognizance of all available information, and a survey of the data from the bionomics, development and morphology has led to the concept advanced in this paper. From a hypothetical, generalized, planula-like ancestor it is possible to derive each of the existing groups of the phylum Platyhelminthes. Comparison of the primitive form with representatives of the Mesozoa shows many resemblances, and if allowance for a long period of parasitism is made, the agreement is remarkable. Moreover, the miracidia of the Digenea and ciliated larvae of the Monogenea can be compared with the ancestral type. In all these groups there is a similarity in cleavage and early developmental stages which clearly denotes genetic relationships. The idea presented appears to be the most natural, logical and satisfactory interpretation of available data.